

A MANDIBLE OF *DIDELPHODON VORAX* (MARSUPIALIA, MAMMALIA)

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ABSTRACT: A fragment of a mandible of *Didelphodon vorax* found in the Hell Creek Formation, Montana, confirms the provisional identification of lower premolars and molars of this species, establishes the orientation of the lower premolars, and serves as the basis for further speculation on the orientation of the upper premolars. The functional significance of prominent lateral lobes on mammalian premolars is examined.

INTRODUCTION

Didelphodon is the largest of the Late Cretaceous marsupials and probably the largest mammal known from any Mesozoic fauna. In addition to its size, the striking modifications of its dentition raise questions concerning the role of *Didelphodon* in the reptile-dominated terrestrial environments of the Cretaceous. When I prepared my study of the marsupials of the Late Cretaceous Lance local fauna (Clemens, 1966), approximately 200 isolated teeth but only seven mandibular fragments of *D. vorax* were available for study. None of these mandibular fragments is as complete as that included in the type of *Didelphodon padanicus* from Late Cretaceous deposits in South Dakota, which contains only two undamaged although heavily worn teeth, the posterior premolar and a questionably associated molar. Also available for comparison is a fragment of an edentulous mandible from the Hell Creek Formation that has been described by Simpson (1927) and can be provisionally identified as representing a species of this genus. The fossil found in the Hell Creek Formation and described in this paper is the most nearly complete mandible of *Didelphodon* yet discovered. It provides significant information correcting and extending previous restorations of the mandible and dentition of *Didelphodon*.

ACKNOWLEDGMENTS

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MATERIAL

Locality: Dr. J. R. Macdonald provided the following information: *Lower Hell Creek no. 1.* Late Cretaceous. Hell Creek Formation. In purple to gray clay and sandy silt, crusty brownish-gray with yellow and brown spots, also some medium-size, round sand concretions and carbonized wood resembling charcoal. Maloney Hill Quadrangle, Garfield County, Montana. Additional locality data are on file at the Los Angeles County Museum of Natural History and available to qualified investigators.

Description: The fossil (LACM 15433) is a fragment of a left mandibular ramus lacking that part of the symphyseal region anterior to the canine. Posteriorly it is broken at the level of the anterior edge of the coronoid process. The root of the canine and alveoli of P_1 are present. P_2 , its apex slightly blunted by wear, and P_3 , which shows less wear, are preserved. M_{1-2} are missing but M_3 , which has large wear facets on the trigonid and talonid, is preserved. Only the trigonid of M_4 , less worn than that of M_3 , remains. The symphysis extends posteriorly to a point below the anterior edge of P_3 . Two mental foramina are present, one below P_{2-3} , the other below M_{1-2} . Measurements of the fossil are given in Table 1.

TABLE 1
Measurements of LACM 15433 in millimeters

	Dentition					
	P_2	P_3	M_3		M_4	
Length	6.5	7.3	6.5			
Width	5.4	4.8	4.8	(trigonid)	4.5 (talonid)	5.4 (trigonid)
	Dentary					
	Below P_3		Below M_3			
Height	14.7		ca. 19.			
Width	8.6		ca. 8.			

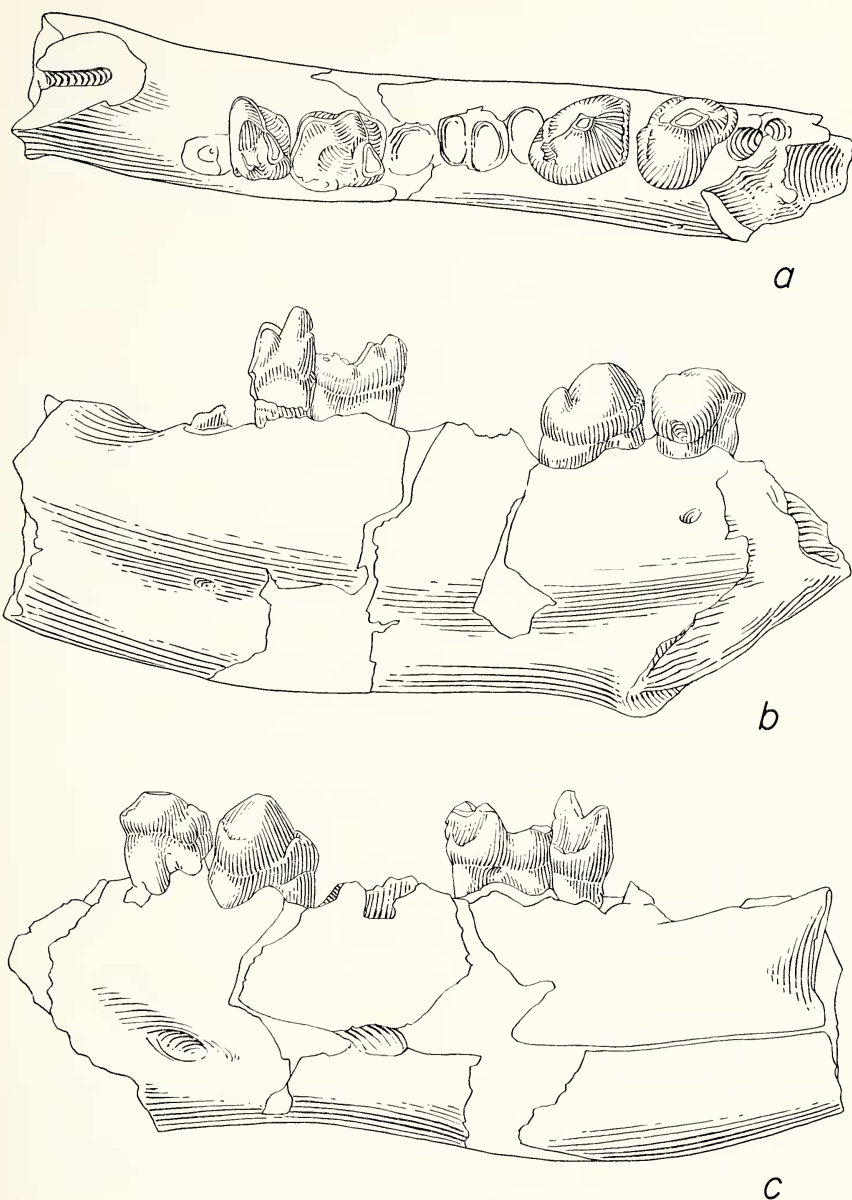


Figure 1. *Didelphodon vorax*, LACM 15433: left mandibular ramus with P_{2-3} , M_3 , and trigonoid of M_1 preserved; *a*, occlusal; *b*, lingual; and *c*, labial views; all X 2.

COMMENTS

In my review of the marsupials of the Lance Formation (Clemens, 1966), two species of *Didelphodon*, the type species *D. padanicus* and *D. vorax*, were recognized. Fossils from the Lance Creek area demonstrate *D. vorax* has three lower premolars of which P_1 is the smallest and P_3 the largest. The evidence afforded by the only known mandible of *D. padanicus* does not clearly document its premolar structure. What remains of the premolars indicates the presence of either four premolars or three premolars with the second being distinctly larger than the last. Differences between species were also observed in morphology of the presumed posterior upper premolars and, possibly, in the smaller size of the teeth of *D. vorax*.

The premolar morphology of LACM 15433 is of the type characteristic of *Didelphodon vorax*. Only three premolars are present. P_2 is smaller than P_3 , although the difference is not so large as would be expected from the isolated teeth in the sample of the Lance local fauna. In only one of its dental dimensions (width of P_2) does the fossil exceed the observed ranges of variation of the Lance sample. The characters of the molars and dentary also support allocation of the fossil to the species *D. vorax*. This discovery extends the range of the species to include the Hell Creek Formation of eastern Montana.

RESTORATION OF THE DENTITION

LACM 15433 permits confirmation of some points in my study (Clemens, 1966) of the lower dentition of *Didelphodon vorax*. These can be summarized as follows: Association of the lower molars and premolars provisionally allocated to *D. vorax* is now demonstrated. The lateral lobes of P_2 and, no doubt, P_1 are on the lingual sides of their crowns. The trigonid of M_1 is labial to the posterior end of P_3 . Although the evidence is still not conclusive, the lower molars appear to have increased in size from M_1 , the smallest, to M_4 . The observed range of the ratios of widths of trigonid/talonid derived from isolated teeth in the Lance sample thought to be M_3 's, 1.07 to 1.13, includes the value of the ratio, 1.07, for the M_3 in LACM 15433.

Using LACM 15433 as a base and selecting teeth collected from the Lance Formation to replace those postcanine teeth missing from it, a partial restoration of the mandible (Fig. 2) has been prepared. The restoration of the canine is based on canines of *Sarcophilus*, and a large isolated canine, YPM 10667, from the Lance Formation described by Marsh (1892, Pl. VIII, fig. 6) and tentatively referred to *Didelphodon vorax*.

In my earlier paper an attempt was made to determine the orientation of the upper premolars of *Didelphodon vorax*, which are known only from isolated teeth. Because of the morphology and apparently regular pattern

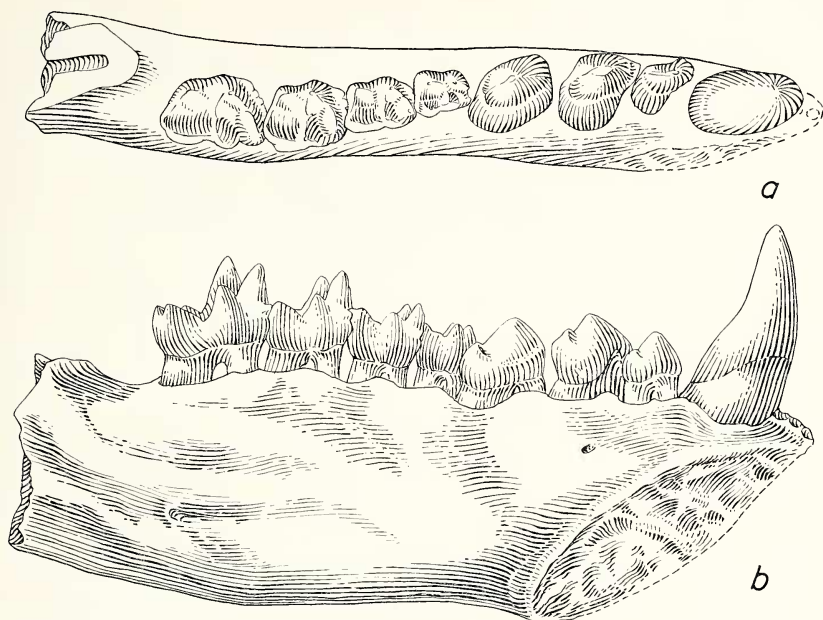


Figure 2. *Didelphodon vorax*; partial restoration of left mandible; a, occlusal, and b, lingual views; both X 1.8.

and sequence in development of wear facets on these teeth, it was assumed the entire battery of lower premolars made contact with the upper premolars. Orientation of the lower premolars with their lobes on the lingual sides of the teeth was supported by some evidence. From study of the wear patterns it appeared to follow that the upper premolars were oriented with the lobes on their labial sides. The orientation was also supported by consideration of the general pattern of symmetry of mammalian dentitions. Although not fully disproving the proposed orientation, several points have come to my attention suggesting that the reverse orientation—the lobes of the upper premolars on the lingual sides of their crowns—is probably correct.

The first restoration of the upper premolars of *Didelphodon* was proposed with the implicit assumption that development of prominent lateral lobes of P_1^{1-2} was the result of selection for increase in the area of contact of the upper and lower premolars. Information obtained from a large series of skulls of *Sarcophilus* (in the Museum of Vertebrate Zoology) supports an alternative assumption.

In gross morphology the lower premolars of *Sarcophilus* (Fig. 3) resemble those of *Didelphodon* and show the same pattern of wear. The

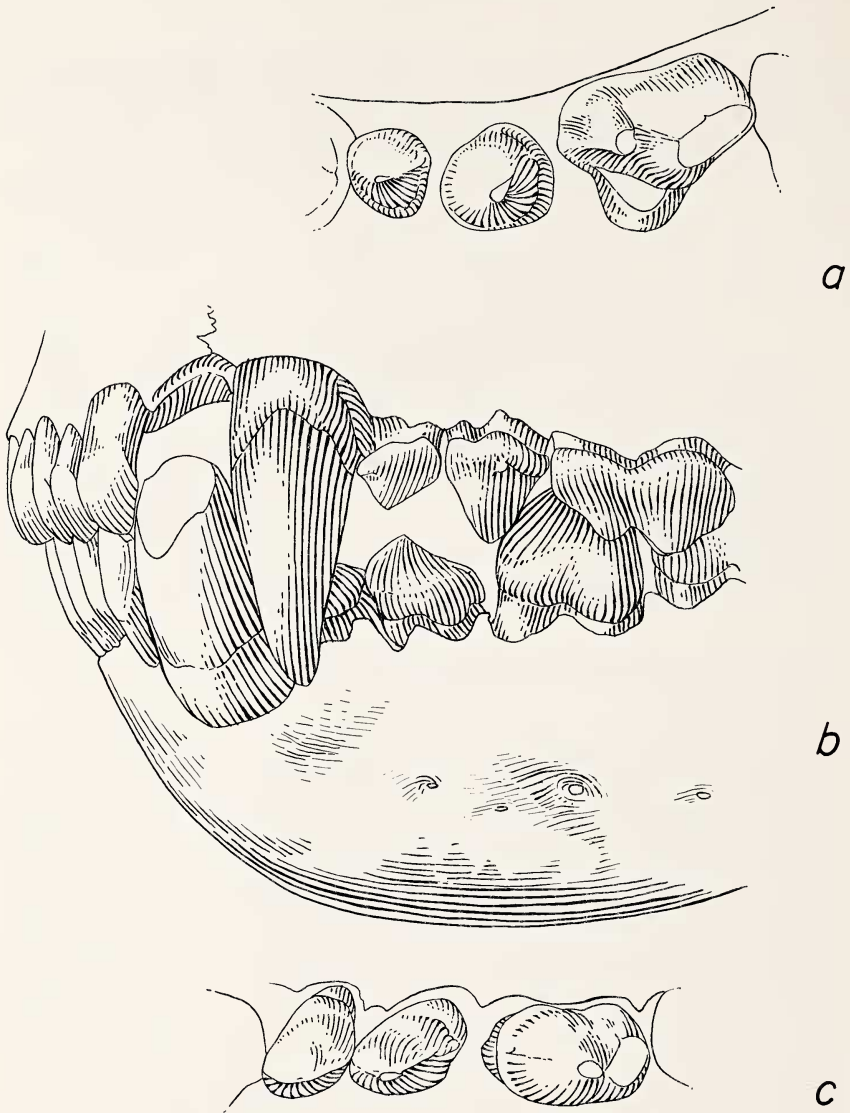


Figure 3. *Sarcophilus harrisi*, MVZ 127035: a, occlusal view, P¹⁻² and M¹; b, lateral view of left upper and lower incisors, canines, premolars, M¹, and part of M²; c, occlusal view, P₁₋₂ and M₁; all X 2.25.

lower premolars of *Sarcophilus* do not contact the uppers when the molars are occluded. P^2 lacks a lobe on the lingual side of its crown. This premolar is situated with the long axis of its crown forming an oblique angle with the midline of the palate and, when the molars are occluded, it lies close to the crown of M_1 . In contrast, in those dentitions of *Sarcophilus* studied, a few P^1 's have a small lingual lobe, but most P^1 's resemble the tooth illustrated here (Fig. 3), which has only a small lingual expansion bordered by a prominent cingulum. Because this cingulum is well removed from the apex of the crown of P_2 when the molars are occluded, it cannot act to increase the area of contact of the upper and lower dentitions.

The convex sides of brachyodont mammalian cheek teeth serve to protect the margin of the gingiva from damage through direct contact with hard or abrasive materials. Because the upper and lower premolars of *Sarcophilus* do not come into contact during occlusion of the molars, development of lobes and cingula on their crowns cannot be attributed to selection for increase of the occlusal area. The modifications probably were developed in response to selection for increase of the area protected by the premolar crowns or change in configuration of the crown to protect the margin of the gingiva.

Similarity in premolar morphology and wear patterns of *Sarcophilus* and *Didelphodon* suggests the assumption that P_{1-2} of *Didelphodon* occluded with P^{1-2} could be erroneous. If these premolars of *D. vorax* did not occlude, the function of their lateral lobes could have been to provide protection for the gingiva, and lobes on the upper premolars could have been on the lingual sides of their crowns. This function and orientation is favored by the presence of steeply inclined wear facets on the lobes of some premolars that might not have developed through contact of upper and lower premolars.

Many extant mammals have premolars with bulbous crowns and, less frequently, lateral expansions or lobes. Restricting comparisons to mammals of approximately the same size—as far as can be determined from mandibular dimensions—the closest resemblance in dental morphology to *Didelphodon* is found in *Sarcophilus* and it is not close. Although the molars (Fig. 4) of the sea otter, *Enhydra*, and *Didelphodon* are distinctly different in function and morphology, their premolars show points of resemblance. The upper and lower first premolars of *Enhydra* usually are lost, but a small peglike P^1 is present in either the upper right or left quadrant of some dentitions (2 of 12 individuals represented in the University of Kansas collections). P_2 and P_3 , which do not occlude with upper premolars, have prominent lobes on the lingual sides of their crowns. The small lobe on the lingual side of P^2 is dorsal to but does not occlude with P_3 . The lobe on the lingual side of P^3 is larger than that of P^2 and has a shallow basin on its surface that receives the apex of P_4 .

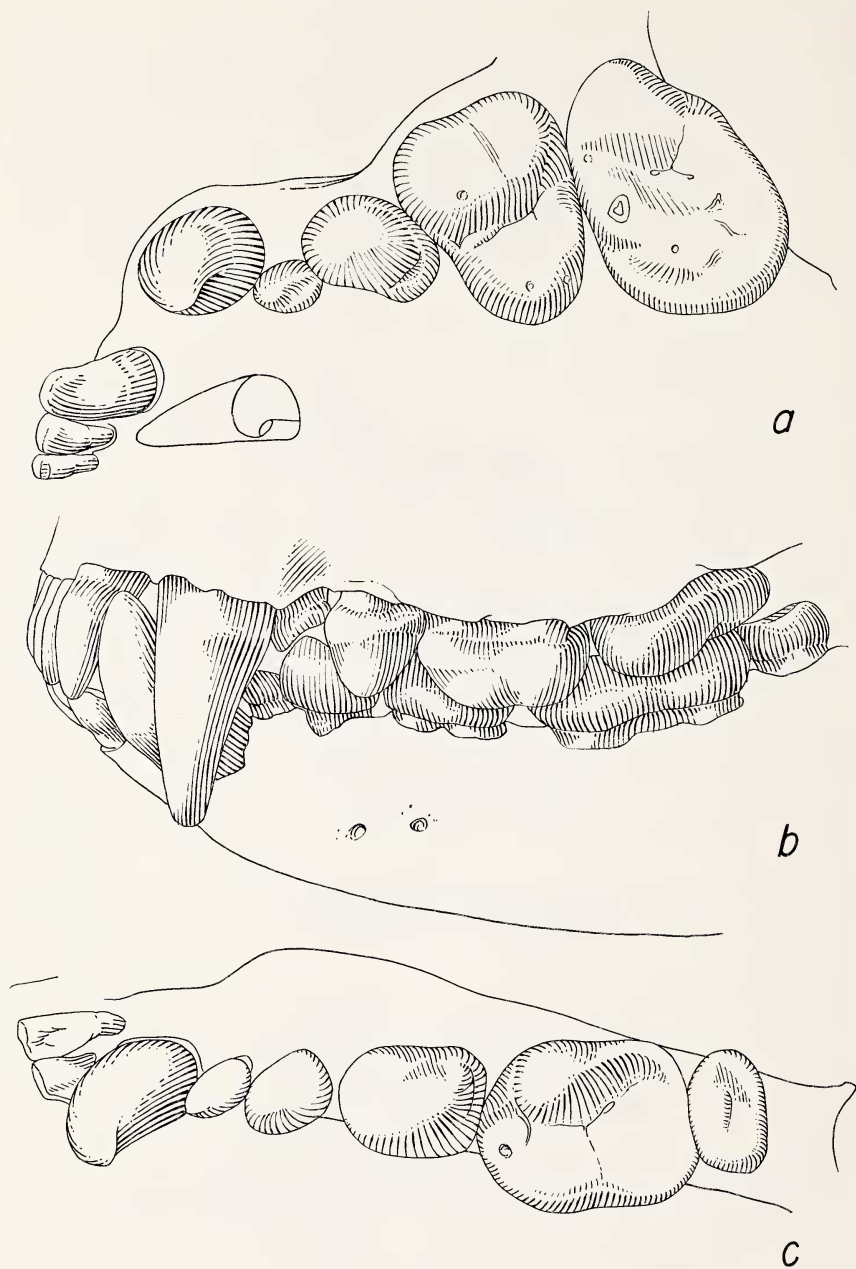


Figure 4. *Enhydra lutris*, KU 44672: a, occlusal view, P²⁻⁴ and M¹; b, lateral view of entire dentition; c, occlusal view, P²⁻⁴, M^{1,2}; all X 2.17.

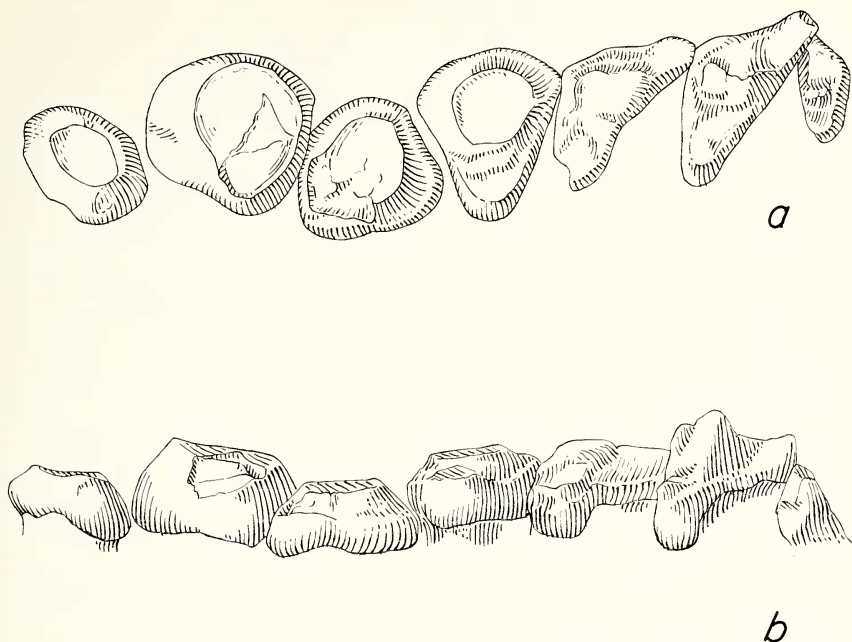


Figure 5. *Quercitherium tenebrosum*, Collections de Paléontologie, Muséum national d'Histoire naturelle, 1893-11: left maxillary fragment with P¹-4 and M¹-3; illustrations based on figures in Piveteau (1935) and cast of fossil; a, occlusal, and b, lingual views; both approximately X 2.

Comparisons can be carried further among placental mammals. The recently established oxyaenoid family, Teratodontidae Savage, 1965, is composed of *Teratodon* and *Quercitherium*. Both have dentitions resembling the dentition of *Didelphodon* in the presence of massive premolars and some shearing molars. Apparently in one species, *Teratodon enigmae*, the first molars also have greatly modified, bulbous crowns. The bulbous teeth of *Teratodon* do not have the prominent lobes found in *Didelphodon*. Savage (1965: 252) suggests the upper and lower premolars of *Teratodon* occluded and were employed in a grinding action.

With the exception of P¹, which has a lingual lobe, the premolars of *Quercitherium* (Fig. 5) more closely resemble those of *Teratodon* than *Didelphodon*. The available casts and illustrations do not reveal whether the wear facets on the premolars of *Quercitherium* are the result of occlusion or apical, non-occlusal wear of the type described by Mac Intyre (1966: 123). However, its position relative to the crowns of other premolars suggests the lingual lobe of P¹ functioned to protect the gingiva.

Because of their position relative to the insertion of the masseter and

the condyle, the massive premolars of *Teratodon* would have obtained little mechanical advantage from the leverage of the mandibular ramus. Savage (1965) noted that functionally the dentition appears to be a compromise between shearing and crushing or grinding functions but one bringing out the worst attributes of both. In teratodontids and *Didelphodon* the lack of great mechanical advantage for the premolars could have been offset by the evolution of a massive masticatory musculature. This modification is found in the jaw musculature of *Sarcophilus*. As Macalister (1872: 18) noted, "The most expressive way of representing the enormous size of these muscles [of *Sarcophilus*] is by stating that the weights of the muscles which elevate the lower jaw (masseters, pterygoids, and temporals) were equal to the sum of the weights of all the scapular and brachial muscles (deltoids, spinates, biceps, brachiales, triceps, & c.), or to the entire series of muscles which act on the shoulder-joint (pectorals, latissimus dorsi, spinati, deltoids, & c.)."

Data obtained from mammals with premolars resembling those of *Didelphodon* suggest the following points concerning the function and orientation of this kind of premolar: Evolution of lateral lobes need not be a response to selection for increase of the occlusal area of the dentition, but may serve to change the configuration of the margin of the gingiva to give it greater protection or increase the area protected by the crowns of the premolars. Presence of these lobes does not necessarily indicate the opposing upper and lower premolars occluded. In all species in which the orientation of the teeth can be definitely established, the lobes are found only on the lingual sides of the upper and lower premolars.

SUMMARY

A fragment of a mandible of *Didelphodon vorax* found in the Hell Creek Formation is described and used as the basis for a restoration of the lower dentition of the species. The morphology of the teeth preserved in this mandibular fragment and evidence from other sources suggests the previously proposed orientation of the upper premolars was erroneous. Prominent lobes on some premolars of *Didelphodon* probably result from selection for increase of the area protected by the premolars or changes in configuration of the crown to protect the margin of the gingiva, not from selection for increase in the area of contact of the upper and lower premolars. Although not fully demonstrated, it now appears most likely that, like the lobes on the lower premolars, those on the upper premolars were also on the lingual sides of their crowns.

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